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Negligible effect of competition on coral colony growth

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Abstract. Competition is an important determinant of assemblage structure and population regulation, often resulting in decreased growth, fecundity or survival. In corals, most studies testing for an effect of competition on demographic traits, such as growth, have been experimental and often impose very high levels of competition upon colonies. To more realistically assess the role of competition on coral traits, multispecies studies in the wild are required. Here, we use 5 yr of data that includes 11 coral species on the reef crest at Lizard Island on the Great Barrier Reef to quantify the effect of competition on growth. Additionally, we test whether species differ in their susceptibility to direct-contact (overgrowth and digestion) and overtopping competition, and whether species from some morphological groups are more likely to compete with one another than with species from other morphological groups. We also investigate the relationships between competitive ability and three key traits: growth rate, mechanical stability and fecundity. In contrast to most previous work using field manipulations of competition, we found a negligible effect of competition on growth. *Acropora* species consistently won overtopping encounters but lost in direct-contact encounters, and these results were consistent among the four *Acropora* morphological groups. In contrast, the massive *Goniastrea* spp. were poor at overtopping but generally won direct-contact encounters. Only tabular colonies were disproportionally more likely to compete against one another than with other morphologies. This propensity increases intraspecific relative to interspecific competition, a phenomenon that can promote coexistence when it is present among dominant competitors. Good competitors grew more quickly and had higher fecundity but were less mechanically stable, implying a tradeoff between performance during disturbance vs. performance in the absence of disturbance. We conclude that competition among adults is less likely to influence community dynamics than previously thought. If competition does have an effect, it is more likely to occur at life-stages other than adults.

Key words: *aggregation; competition; coral; demographic rates; growth; morphology; tradeoff.*

Introduction

The effect of competition on individuals' fitness can affect community structure and dynamics. Competition occurs when two individuals consume common limiting resources, and it can reduce individual fitness by reducing the resource to sub-optimal levels (exploitation competition) or by reducing the competitor's access to the resource (interference competition). If one of the competitors is more efficient at exploiting the resource, competition can result in the local extinction of the weaker competitor (Gause 1934, Tilman 1982). Even when extinction does not occur, manipulative studies that have removed dominant species show that the subordinate species usually occupies areas that were previously occupied by the superior competitor (Paine 1966, Martin and Martin 2001). The energetic cost of competition can result in reductions in growth, fecundity or maintenance at the individual level, and the joint effect of competition on individuals in a community influences community structure (e.g., barnacles: Connell 1961, sea stars and mussel: Paine 1966, birds: Martin and Martin 2001). Understanding the effects of competition at the individual level is therefore necessary to predict changes in community composition.

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Competition among benthic organisms for space can influence species abundance and richness (Chadwick and Morrow 2011). For corals, space is the main limiting resource and the capture of space provides access to other resources, such as nutrients and light. Competitive interactions among established adult colonies tend to be complex for various reasons. First, coral colonies can compete against each other through direct-contact competition by digesting or overgrowing competitors, or without direct contact through overtopping (Fig. 1a). Taxa and colony morphologies that are good competitors in direct-contact competition tend to lose in overtopping competition and vice-versa (Lang and Chornesky 1990). Secondly, species competitive rankings are not strictly hierarchical and competitive outcomes are often inconsistent and can reverse over time (Bak et al. 1982, Lang and Chornesky 1990, Precoda et al. 2017). Additionally, size asymmetry between competitors influences competitive outcomes, favoring colonies of larger size (Zilberberg and Edmunds 2001). Competitive outcomes are therefore difficult to predict.

Competition among adult colonies generally results in inferior demographic rates. For example, colony growth is reduced when in competition against other corals (Romano 1990, Tanner 1997) or against algae (Tanner 1995, Lirman 2001, Box and Mumby 2007, *but see* Jompa and McCook 2002, Lapid and Chadwick 2006). However,

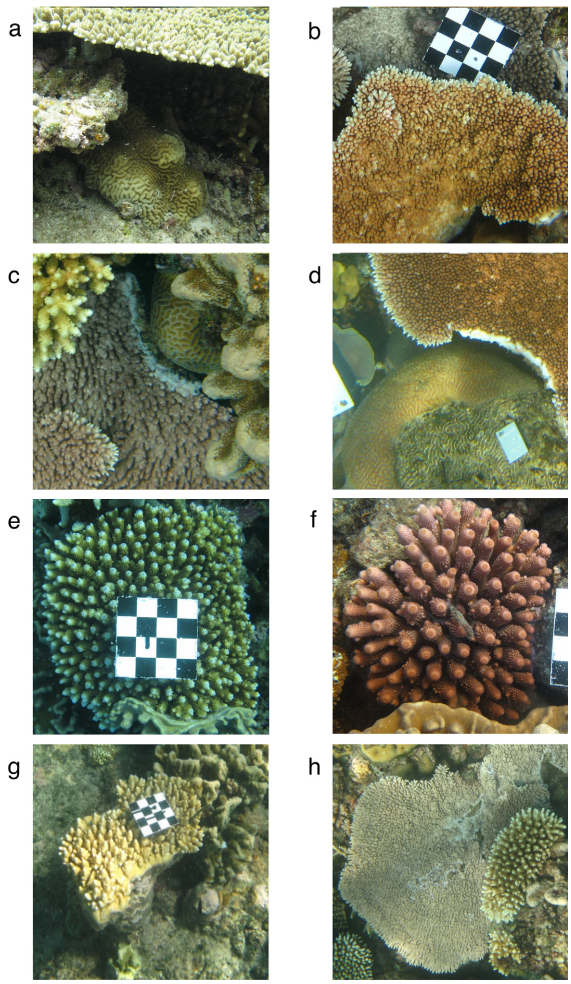

FIG. 1. Photographs of competing colonies. (a, b) Tabular colonies overtopping competitors. (c, d) Tabular colonies being digested by massive neighbours. (e, f) A corymbose and a digitate colony being overgrown by a soft coral. (g, h) Elevated microhabitats of digitate colonies.

studies that manipulate competition often create extremely high levels of competition (e.g., by fastening colonies to one another), which are only true for a small subset of competitive interactions. Additionally, in the central Indo-Pacific, assemblages are often species-rich with many different colony morphologies. In particular, there are numerous rapidly growing branching species that compete through overtopping. Consequently, overtopping rather than direct-contact competition might be the dominant competitive mechanism on most reefs (Sheppard 1979). The effect of competition between coral colonies on colony growth under such natural conditions remains poorly understood.

Competitive abilities are commonly linked to traits (e.g., in plants: Goldberg and Landa 1991), and tradeoffs can arise when traits favoring competitive abilities come at a cost to other ecological functions. Tradeoffs between competitive ability, stress tolerance, tolerance to disturbance and reproductive output have long been proposed (MacArthur and Wilson 1967, Grime 1977) and are evident in various organisms (e.g., *fish:* Dunson and Travis 1991, *plants:* Angert et al. 2009, *molluscs:* Krassoi et al. 2008). For scleractinian corals, colony morphology is recognised as an important trait affecting competitive ability (Lang 1973, Connell et al. 2004, Precoda et al. 2017), and demographic rates differ between different colony morphologies (Madin et al. 2014, Álvarez-Noriega et al. 2016, Dornelas et al. 2017). Colony morphology is highly correlated with colony growth (Dornelas et al. 2017), and fast growth rates should lead to victory in most overtopping encounters; in contrast, massive competitors are more aggressive in direct-contact competition (Lang 1973).

Tradeoffs can arise if high competitive abilities are linked to inferior demographic rates in some colony morphologies or species. Tradeoffs between competitive abilities and important demographic rates might prevent the best competitors from displacing subordinate species. However, for overtopping competition, competitively superior species often have higher growth rates than competitively inferior species; at least in some areas of the reef (Connell et al. 2004). In scleractinian corals, the relationships between competitive ability and other demographic rates are yet to be quantified.

Spatial arrangements in the community determine which individuals compete against each other, and can have important implications for community dynamics (Levins and Culver 1971, Tilman 1994). Aggregation of dominant conspecifics benefits subordinate species by increasing the number of intraspecific competitive encounters relative to interspecific ones, and thereby reducing competitive encounters between dominants and subordinates (Harper 1977) and reducing interspecific competition overall (Klopfer and Ives 1997). Spatial aggregation of conspecifics can facilitate coexistence under some circumstances, even though it is not a coexistence-promoting mechanism itself (Chesson and Neuhauser 2002). For example, in species with planktonic dispersal, coexistence is promoted when the dominant competitor forms conspecific clusters at settlement, leaving patches of free space where inferior competitors can establish (Bolker and Pacala 1997). On coral reefs, some species form conspecific aggregations (Sheppard 1980, Chadwick and Morrow 2011), and abundant species tend to be more aggregated than rare species (Karlson et al. 2007), a pattern also observed in plants (He et al. 1997). If, as a result, superior competitors in coral assemblages experience elevated intraspecific competition, then coexistence with weaker competitors might be promoted.

Here, we first quantify the change in coral colony growth caused by competition, and we test whether species (or colony morphologies) differ in their competitive abilities depending on the type of competition. We then investigate the relationship between species' competitive abilities and colony fecundity, growth and susceptibility to mechanical dislodgement. We hypothesize that: (1) colonies experiencing more competition will grow at a slower rate than colonies experiencing less competition; (2) competitive outcomes depend on colony morphology and type of competition (direct-contact or overtopping); (3) colonies are more likely to compete with a colony of the same morphology than expected by chance; and (4) tradeoffs emerge between competitive ability and at least one other demographic rate.

Methods

Study location and data collection

To test our hypotheses, data were collected on the semi-exposed reef crest of Lizard Island in the north of the Great Barrier Reef (GBR; 14.699839° S, 145.448674° E). In 2008, 30 colonies from each of 11 species belonging to five morphologies were tagged (depth ranging from 1 to 2 m): arborescent (*A. intermedia* and arborescent encrusting: *Acropora robusta*), corymbose (*A. nasuta, A. millepora* and *A. spathulata*), digitate (*A. humilis* and *A. cf. digitifera*), massive (*Goniastrea pectinata* and *G. retiformis*), and tabular (*Acropora cytherea* and *A. hyacinthus*). For each species, an effort was made to collect colonies from the entire range of colony sizes found at the site, without regard to the amount of competition they were experiencing (see Appendix S1: Fig. S1). Thus, we expect competition levels in our samples to be representative of competition levels experienced by each species at our study site. Coral cover on the reef crest was estimated using 10 by 10 m line intercept transects in 2011 at 40 ± 3.0% (mean ± SE). The colonies were followed through time, and photographed from above with a scale plate every year from 2009 to 2013 (Madin et al. 2014, Álvarez-Noriega et al. 2016, Dornelas et al. 2017).

The photographs were corrected for barrel distortion, and the perimeters of the focal colonies were digitally traced to estimate colony area (planar area) and colony perimeter using ImageJ (Bethesda, Maryland, USA). Additionally, the starting and ending points of contact in a competitive interaction were marked on top of the digital image of the colony's perimeter, to measure the proportion of the colony's periphery involved in competitive interactions. The competitive contacts were classified as overtopping, digestion or overgrowth. An encounter was scored as overtopping when either the focal colony or a neighbor were partially covering the other colony on the planar view (Fig. 1a, b). Colonies can also digest nearby colonies that are within the reach of their extruded mesenterial filaments, leaving a white border or injury in the area of contact (Lang 1973). An encounter was scored as digestion when either colony had a white border or injury near the margin of another colony (Fig. 1c, d). An encounter was scored as overgrowth if one of the colonies was growing on the surface of the other colony (Fig. 1e, f). Encounters scored as digestion or overgrowth were grouped together as "direct-contact" encounters because there were few observations of both competitive mechanisms. Interactions were not considered competitive when colonies were in close proximity but with no signs of digestion, overgrowth or overtopping (i.e., standoffs). Growth was estimated as the change in colony planar area between consecutive years on a log-scale (log[area in cm^2 at time $t + 1$]−log[area in cm^2 at time t]). Change in planar area is a common measurement for growth because it represents the amount of space (the potentially limiting resource) acquired by an organism in an interval of time (e.g. Connell et al. 1997, 2004). Measuring growth as a change in planar area fails to account for vertical growth (Pratchett et al. 2015), which is particularly common in massive species (Lough and Barnes 2000). Thus, if growth in planar area decreases in response to competition, it could be due either to reduced growth overall, or redirection of growth in a vertical direction.

Statistical analysis

Effect of competition on growth .—We fitted a linear quantile regression to estimate colony growth as a function of colony size, species, competition (as the proportion of the colony's periphery in competition) and the interaction between species and competition. From this main model, we fitted subsequent models with each possible combination of a subset of explanatory variables, and we selected the best-fit model by using Akaike weights (from the package "qpcR"; Spiess 2015). Following Dornelas et al. (2017), each set of models was fitted through the 95th, 50th and 5th quantile of colony growth. The 95th quantile captures the growth of the fastest-growing colonies (which we take to represent colonies in optimal conditions, i.e., maximum potential growth). Conversely, the 5th quantile captures the slowest-growing (often shrinking) colonies, which we take to represent colonies exposed to the highest levels of partial colony mortality. The 50th quantile is the median growth, which we take to represent growth under typical conditions and levels of natural mortality. It seems unlikely that winning overtopping competitive encounters (i.e., successfully overtopping another colony) would negatively affect colony growth of the winner. Therefore, we measured competition as the proportion of the focal colony's periphery being overtopped or in a direct-contact competitive encounter. Qualitative results were unchanged when standoffs were included in the analysis. Only a subset of models was fitted through quantiles 95th and 5th due to problems with convergence. The models were fitted using the R-package "quantreg" (Koenker et al. 2017).

Predictability of competitive outcomes .—We used a binomial regression to predict the probability of winning an overtopping encounter for each species (using the package "rstanarm"; Stan Development Team 2016). Since each tagged colony could have up to five observations (one per year), we included colony identity as a random intercept (with the function "stan_glmer"). Similarly, we fitted another binomial regression to predict the probability of winning a direct-contact competitive encounter with species as the explanatory variable and again with colony identity as a random intercept. To test the effect of colony identity on the outcome of competitive interactions, we fitted two more binomial regressions: one for overtopping interactions and one for direct-contact competitive interactions, this time without colony identity as a random intercept (with the function "stan_glm"). We compared the models with and without colony identity using leave-one-out cross-validation, and calculating the difference in the expected log predictive density (ELPD) of the models and the standard error associated with this difference (Vehtari et al. 2016). A negative ELPD indicates that the expected predictive accuracy of the first model is higher than that of the second one. A better fit of the model with colony identity as a random effect compared to the model without colony identity would indicate that the competitive outcomes for individual colonies were

consistent among competitors and through time (i.e., if a colony was winning against one competitor at time *t,* it is disproportionately likely that it will also be winning against other competitors, and at other times). We would expect such a pattern if, for instance, a colony's position on the reef, or its height relative to its planar area, gave it a competitive edge. We identified competitors to genus level, but we later grouped competitors according to their colony morphologies due to low replication in most genera. Only coral-coral interactions were included, since interactions with macroalgae and sponges were rare.

Intraspecific vs. interspecific competition.—We used a generalized linear model with a binomial error structure to predict the probability of a competitive interaction being with another colony of the same morphology. The response variable was the competitor's morphology (same as focal colony's or different). We did this analysis separately for each focal morphology.

Relationship between performance in overtopping competition and demographic rates.—Given that overtopping competition was commonly observed and direct-contact competition was rare, we used the species' performance in overtopping competition as a proxy for competitive ability. We used a non-parametric Spearman's rank correlation ρ to test for a correlation between the probability of winning a competitive encounter that involves overtopping and four demographic rates: colony growth, mechanical vulnerability, reproductive investment and number of oocytes per colony at the species level. Mechanical vulnerability was measured by the colony shape factor (CSF; Madin and Connolly 2006), which is a dimensionless quantity that depends on colony size and colony shape. An increase in CSF corresponds to an increase in mechanical vulnerability. CSF values decrease with increasing colony base width (i.e., bottom-heavy) and increase with increasing colony width above the base (i.e., top-heavy). We estimated CSF values for the largest colonies observed in this study using the CSF regressions in Madin et al. (2014). Reproductive investment and number of oocytes per colony are proxies for colony fecundity. Reproductive investment takes into account the estimated number of oocytes produced per colony and their energy (carbon) content. We estimated reproductive investment and number of oocytes from regressions of reproductive investment vs. colony sizes and of number of oocytes vs. colony size in Álvarez-Noriega et al. (2016) for the range of observed colony sizes, and we calculated the mean values for each proxy. Note that regressions were only available for eight out of the 11 species in this study, and that fecundity measurements were taken at the site but from different colonies than those in this study, because sampling for fecundity in corals is destructive (branches must be broken off of the colony) and such injuries can affect subsequent colony growth.

To account for differences between *Acropora* and *Goniastrea* species, we tested the correlation between the probability of winning an overtopping competitive encounter and the demographic rates with all species, and then again only for the *Acropora* species. All analyses were performed in R (R Core Team 2016).

Results

Although competition was an explanatory variable in the best-fit models predicting colony growth (Appendix S1: Table S1), competition did not significantly reduce potential colony growth, realized net colony growth or growth under severe partial mortality (Table 1). *Acropora* species are more likely to win a competitive encounter that involves overtopping, regardless of their colony growth form, whereas *Goniastrea* species are not (Fig. 2a), but their probability of winning a direct-contact competitive encounter is generally low (Fig. 2b). In contrast, *Goniastrea* species perform poorly in overtopping competition (Fig. 2a), but have very high probabilities of winning in direct-contact competition (Fig. 2b). Overtopping was the most prevalent type of competition, being over seven times more common than direct-contact competitive encounters (2045 vs. 275 competitive encounters observed). Most of the 11 species had overtopping interactions with all competitor groups (Fig. 2a), while direct-contact interactions mostly occurred with only a subset of competitor groups for most species (Fig. 2b), possibly due to the lower number of direct-contact interactions. For example, *G. pectinata* competed without direct contact with all competitor groups, but only directly with tabular *Acropora* species.

Colony identity was an important factor determining overtopping competitive outcomes only. Colonies tended to be more consistently "winners" or "losers" in overtopping encounters than the estimated average for the species. In contrast, there was no colony-level random effect in the outcome of direct-contact encounters (i.e., colonies did not tend to be more consistently winners or losers than average for their species). The difference in expected log predictive density (ELPD) between the model with colony identity as a random effect and the model without random effects for overtopping competition was -61.8 ± 11.6, indicating that the first model had a better fit than the second one. In contrast, for direct-contact competition the best fit did not include colony identity as a random effect (ELPD: 16.9 ± 11.5).

Table 1. Coefficient estimates of the best-fit models predicting the 5th, 50th, and 95th quantiles of colony growth with quantile regression. Standard errors were computed using bootstrapping techniques. Bold letters indicate the significant effects for each regression.

	Coefficient	SE	*t* value	Pr(>|*t*|)
Quantile 0.05				
Intercept	**−0.704**	**0.214**	**−3.290**	**0.001**
Log (area)	0.016	0.030	0.543	0.588
Competition	0.284	0.154	1.842	0.066
Quantile 0.50				
Intercept	**0.401**	**0.093**	**4.326**	**<0.001**
Log (area)	**−0.076**	**0.014**	**−5.447**	**<0.001**
Competition	0.186	0.198	0.939	0.348
Quantile 0.95				
Intercept	**2.319**	**0.522**	**4.440**	**<0.001**
Log (area)	**−0.252**	**0.069**	**−3.645**	**<0.001**
Competition	−0.415	0.545	−0.761	0.447

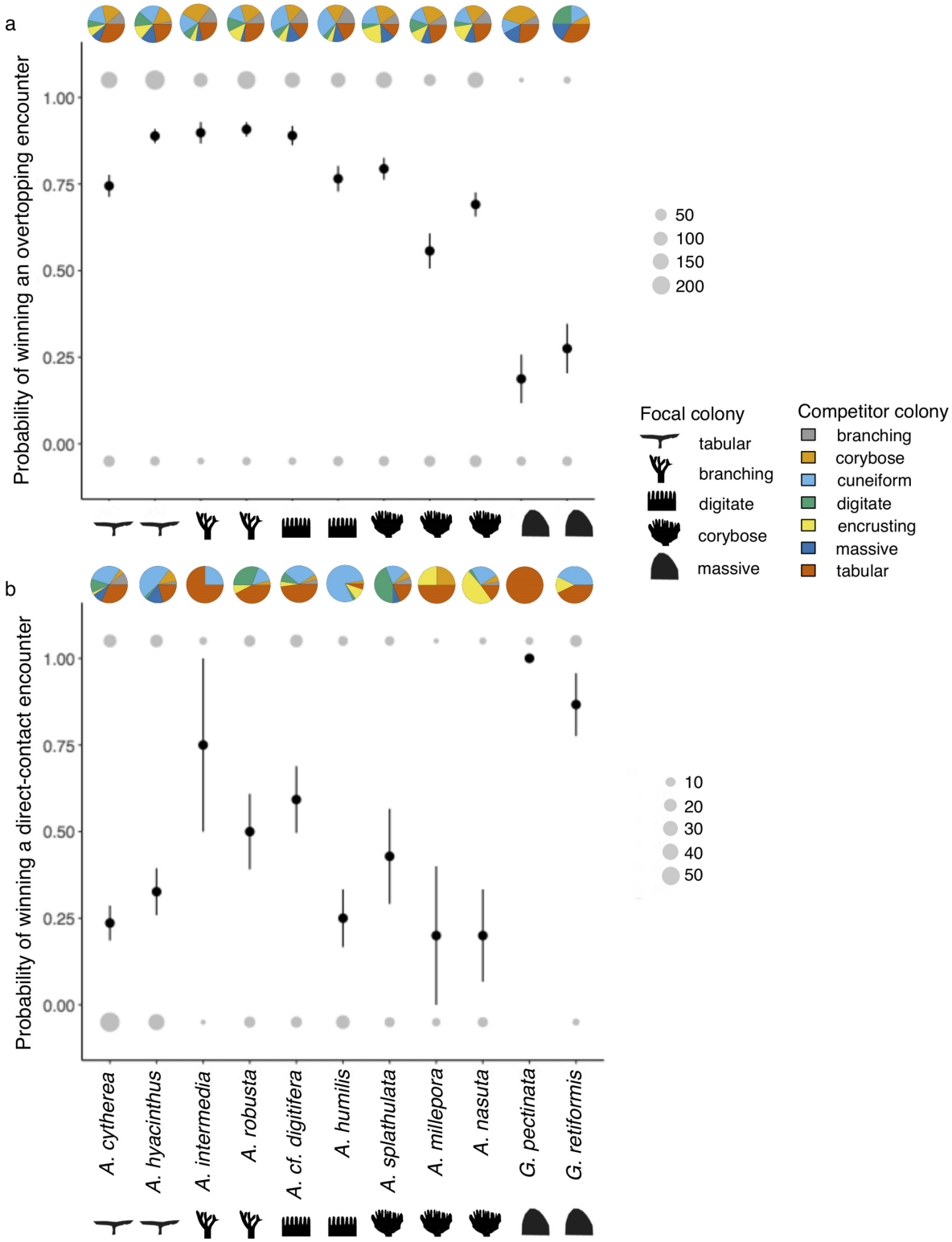

FIG. 2. Probability of winning competitive encounters. (a) Probability of winning an overtopping competitive encounter for each species. (b) Probability of winning a direct-contact competitive encounter for each species. Line ranges indicate standard errors. The pie charts show the distribution of the competitors' colony morphology. The grey points correspond to the data and their size is proportional to the number of observations. Note that their size represents different number of counts for the probability of winning an overtopping competitive encounter and for the probability of winning a direct-contact competitive encounter. Points were displaced slightly below 0 (for encounters lost) and slightly above 1 (for encounters won) to avoid overlap with estimates and credible intervals.

Colonies that were good overtoppers were also fast growing (Fig. 3a), vulnerable to dislodgement (Fig. 3b) and highly fecund (Fig. 3c, d). However, the correlation was only significant between overtopping, mechanical vulnerability (CSF) and maximum reproductive investment when including the *Goniastrea* species (Table 2).

Tabular colonies were disproportionally more likely to compete with other tabular colonies than with colonies of other morphologies, but other morphologies did not compete disproportionately more often with colonies of the same morphology (Fig. 4, Appendix S1: Table S2).

TABLE 2. Spearman's rank correlation results for the relationships between the different demographic rates and the mean probability of winning an overtopping competitive encounter, first including the two *Goniastrea* species and then with *Acropora* species only.

	Including *Goniastrea* spp.		*Acropora* spp. only	
	P-value	ρ	*P*-value	ρ
Growth vs. overtopping probability	0.107	0.518	0.744	0.133
CSF vs. overtopping probability	0.010	0.755	0.121	0.567
Reproductive investment vs. Overtopping probability	0.028	0.782	0.356	0.486
Number of oocytes vs. Overtopping probability	0.096	0.643	0.564	0.314

DISCUSSION

Despite previous findings showing a reduction in growth with competition for at least some species (Karlson 1978, Romano 1990, Tanner 1997) competition between corals did not reduce colony growth on the reef crest of Lizard Island on the GBR. The intensity of competition is likely to be affected by many factors, in particular coral cover. Competitive encounters are likely to be more frequent at a higher coral cover because there is a greater chance of colonies' edges overlapping. Additionally, competition levels also fluctuate through time, being less intense shortly after a major disturbance and more intense as populations recover. Coral cover at our study site on Lizard Island at mean of 40 ± 3.0% was considerably higher than the mean

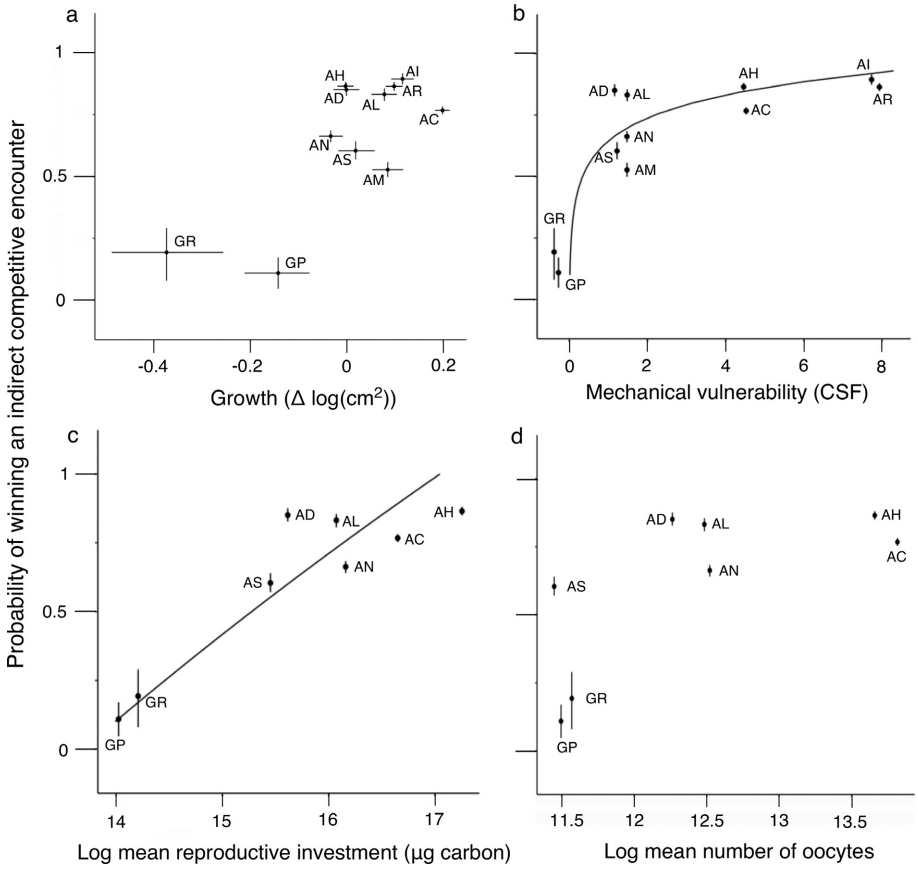

FIG. 3. Relationships between overtopping competitive ability and key demographic traits. (a) Mean colony growth rate [log(area in cm^2 at time t + 1)−log(area in cm^2 at time t)] vs. the probability of winning an overtopping competitive encounter. (b) Mechanical vulnerability (CSF) of the largest colonies vs. the probability of winning an overtopping competitive encounter. (c) Mean reproductive energy investment per colony (carbon content in μg; log-scale) vs. the probability of winning an overtopping competitive encounter. (d) Mean number of oocytes per colony (log-scale) vs. the probability of winning an overtopping competitive encounter. The line range and domain correspond to the 95% credible intervals. Labels indicate species (GR- *G. retiformis*, GP- *G. pectinata*, AN- *A. nasuta*, AS- *A. humilis*, AM- *A. millepora*, AD- *A. cf. digitifera*, AL- *A. spathulata*, AC- *A. cytherea*, AH- *A. hyacinthus,* AR- *A. robusta*, and AI- *A. intermedia*). Lines show the fitted inverse exponential functions when the correlation is significant.

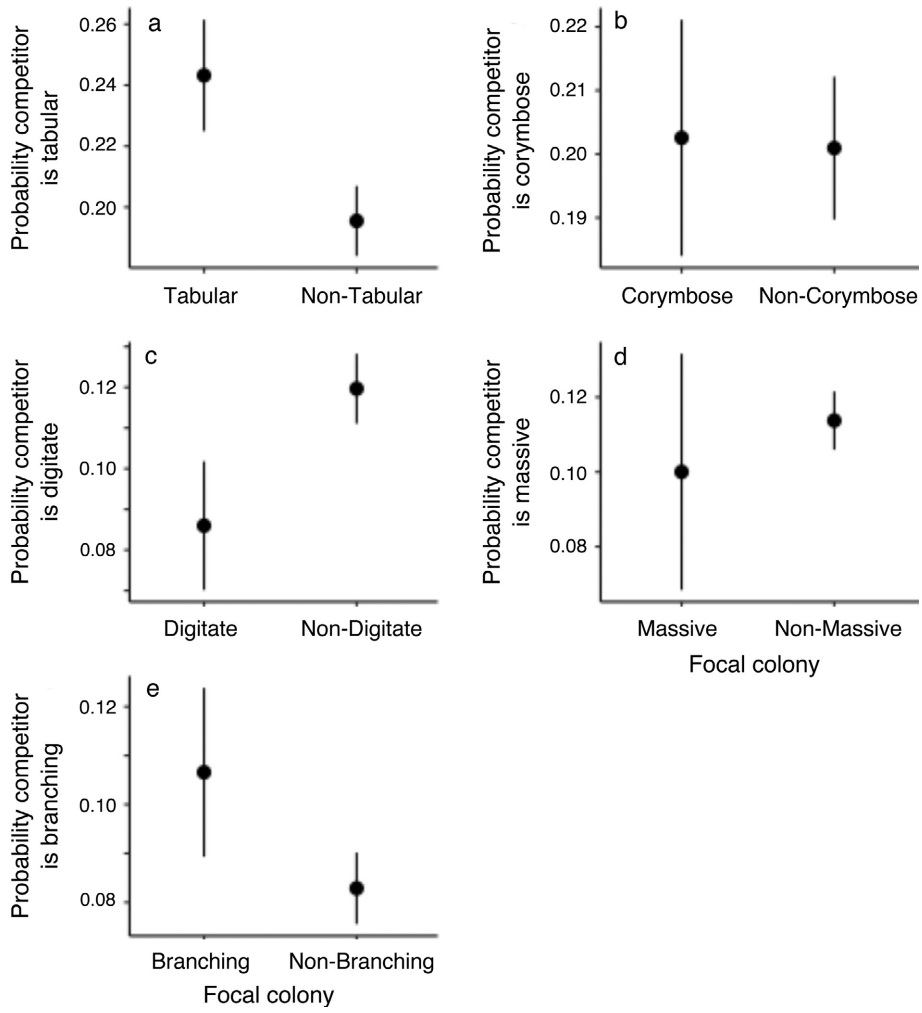

FIG. 4. Intra- vs. inter-morphological group competition. (a) Probability of a competitor having a tabular morphology if the focal colony has a tabular morphology vs. other morphology. (b) Probability of a competitor having a corymbose morphology if the focal colony has a corymbose morphology vs. other morphology. (c) Probability of a competitor having a digitate morphology if the focal colony has a digitate morphology vs. other morphology. (d) Probability of a competitor having a massive morphology if the focal colony has a massive morphology vs. other morphology. (e) Probability of a competitor having a branching morphology if the focal colony has a branching morphology vs. other morphology. Line ranges indicate standard errors.

of 29% on reef crest along the length of the Great Barrier Reef between 1995 and 2009 (Osborne et al. 2011). While our data set only captures a 5-yr window of the successional sequence of competition levels, given the relatively high level of coral cover, it is likely that competition in our study is more intense than its temporal average. The lack of an effect of competition on growth does not necessarily imply that competition has no role in community dynamics. For example, competition might negatively affect demographic rates other than growth, such as reproduction (*but see* Tanner 1997) or survivorship, particularly if competing colonies are maintaining growth at the cost of lower skeletal density and therefore greater susceptibility to mechanical disturbance. Furthermore, competition for space can also occur between adult colonies and recruits via pre-emption of space by adults, and among recruits. We hypothesize that competition among these life history stages affect community dynamics more strongly than competition among adults, particularly since recruitment success fluctuates idiosyncratically (Hughes et al. 1999, Adjeroud et al. 2007).

The competitive performance of corals was consistent among corals of the same genus. Good performance by corals in one type of competition came at the cost of performance in the other type of competition. That is, *Acropora* colonies had high probability of winning an overtopping interaction but also high probability of losing a direct-contact interaction, and the opposite was true for *Goniastrea* species. Surprisingly, there were no clear differences among *Acropora* colony morphologies. Considering that branching and tabular colonies have branches that extend much farther out from the base than digitate and corymbose colonies, we expected that the former would be better overtoppers than the latter. This counter-intuitive result can be partially explained for digitate colonies by their microhabitat: they were commonly located on elevated areas of the reef crest and would commonly grow and extend out into the water column (Fig. 1g, h).

In contrast to coral assemblages with very low abundances of *Acropora*, where digestion is the most common type of interaction (e.g. the Caribbean: Lang 1973, Gulf of Mexico: Ferriz-Domínguez and Horta-Puga 2001), overtopping competition is vastly more prevalent than direct-contact competition at our site on the GBR. Consequently, fast-growing *Acropora* spp. with complex colony morphologies had a competitive advantage over their competitors, whereas slow-growing massive *Goniastrea* spp. did not. However, as indicated by the better fit of the model with colony identity as a random effect, indirect competitive outcomes were affected by the particular conditions of individual colonies: some colonies were consistently more likely than average for their species to be successfully overtopping their competitors, while other colonies of the same species were less likely than average to be overtopping their competitors. Such differences among colonies of the same species could represent differences in position on the reef (e.g., frequent winners might be growing on substrate that is slightly elevated, relative to the surrounding substrate), or differences in colony shape (e.g., frequent winners are somewhat taller than average, given their size).

Tabular colonies were more likely to compete against conspecifics than expected by chance. Tabular colonies grow fast (Dornelas et al. 2017) and can kill conspecifics placed in their shade (Baird and Hughes 2000) and sometimes dominate large areas of the reef, forming low-diversity zones (Done 1982). Aggregation of superior competitors can allow inferior competitors to persist in the community by leaving free space to colonize or rapidly exploit if there is a tradeoff between competition and colonization or between competition and rapid exploitation (Bolker and Pacala 1997). However, the negligible effect of competition on growth suggests that aggregation of competitive dominants is unlikely to promote persistence of inferior competitors by increasing intraspecific relative to interspecific competition between adult colonies (*but see* Idjadi and Karlson 2007). Nevertheless, aggregation of conspecific dominants could be coexistence-promoting through competition between adults and recruits (Baird and Hughes 2000, Vermeij 2005, Marhaver et al. 2013). Furthermore, if settlement processes produce aggregations of superior competitors, conspecific settlers might suffer density-dependent mortality (Vermeij et al. 2009, Doropoulos et al. 2017) that will limit population growth.

Good performance in overtopping competition was associated with higher mechanical instability. Tradeoffs are important because they can reduce differences in fitness between competitors (Chesson 2000), and thereby promote or maintain species richness. For example, branching colonies have high probabilities of overtopping massive colonies but they are also more easily dislodged by strong wave action, which then releases massive colonies from competition. The tradeoff between competitive abilities and mechanical stability in corals has long been proposed (Connell 1978), but not tested. However, this tradeoff may not have important consequences at the assemblage level if the amount of competition experienced in the field does not materially affect colonies' demographic rates. Although the tradeoff between competition and mechanical stability was only significant when including *Goniastrea* species, a moderate positive relationship was still present when only the *Acropora* species were included, and it would be interesting to test if the tradeoff holds when including a broader range of taxa. In contrast to the negative relationship between overtopping competitive ability and mechanical stability, the positive relationship between overtopping competitive ability and reproductive investment means that the best competitors also invest the most in reproduction, thereby increasing differences in fitness between species. While this relationship holds at the species level, it is possible that individual colonies reduce investment into reproduction in the presence of competition. The positive relationship between overtopping competitive ability and reproductive investment diverges from traditional plant ecology, where fast growth and high fecundity are typically associated with "weedy," or "ruderal", life-history strategies, which are also characterized by poor competitive ability (Grime 1977).

Competition is typically thought to be one of the major factors limiting population growth and shaping community structure. Here, we show that adult growth is density-independent for realistic levels of crowding in coral assemblages — a system where competition is typically thought to be important. Additionally, we show that there is a tradeoff between overtopping and direct-contact competitive abilities, but competitive outcomes depend on the particular conditions of competitors. The absence of an absolute competitive dominant and the lack of a negative effect of competition on an important demographic rate suggest that that competition between adults is less likely to influence coral community dynamics than previously thought, and that density-dependent processes like competition may be more important at other life-stages of corals.

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